



Background visual cues and memory-guided reaching

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Abstract

Recent research [e.g., Carrozzo, M., Stratta, F., McIntyre, J., & Lacquaniti, F. (2002). Cognitive allocentric representations of visual space shape pointing errors. *Experimental Brain Research* 147, 426–436; Lemay, M., Bertrand, C. P., & Stelmach, G. E. (2004). Pointing to an allocentric and egocentric remembered target. *Motor Control*, 8, 16–32] reported that egocentric and allocentric visual frames of reference can be integrated to facilitate the accuracy of goal-directed reaching movements. In the present investigation, we sought to specifically examine whether or not a visual background can facilitate the online, feedback-based control of visually-guided (VG), open-loop (OL), and memory-guided (i.e. 0 and 1000 ms of delay: D0 and D1000) reaches. Two background conditions were examined in this investigation. In the first background condition, four illuminated LEDs positioned in a square surrounding the target location provided a context for allocentric comparisons (visual background: VB). In the second condition, the target object was singularly presented against an empty visual field (no visual background: NVB). Participants ($N = 14$) completed reaching movements to three midline targets in each background (VB, NVB) and visual condition (VG, OL, D0, D1000) for a total of 240 trials. VB reaches were more accurate and less variable than NVB reaches in each visual condition. Moreover, VB reaches elicited longer movement times and spent a greater proportion of the reaching trajectory in the deceleration phase of the movement. Supporting the benefit of a VB for online control, the proportion of endpoint variability explained by the spatial location of the limb at peak deceleration was less for VB as opposed to NVB

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reaches. These findings suggest that participants are able to make allocentric comparisons between a VB and target (visible or remembered) in addition to egocentric limb and VB comparisons to facilitate online reaching control.

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1. Introduction

The vast majority of goal-directed reaching studies contrasting visually and memory-guided movements have done so in the context of a target presented in an otherwise neutral or empty visual background (e.g., Carlton, 1981; Elliott, 1988; Elliott & Madalena, 1987; Heath & Westwood, 2003; Heath, Westwood, & Binsted, 2004; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Westwood, Heath, & Roy, 2001, 2003; Woodworth, 1899). From this work, it has generally been shown that visually guided actions are more accurate and less variable than memory-guided ones (Elliott et al., 1999; Flanders, Tillery, & Soechting, 1992; Heath & Westwood, 2003; Heath et al., 2004; McIntyre, Stratta, & Lacquaniti, 1998; Westwood et al., 2001). Presumably, that is because vision of the aiming environment (including limb and target) allow the performer to specify movement parameters in an egocentric visual frame of reference and evoke visually based limb/target amendments (see Elliott, Helsen, & Chua, 2001 for a historical review). When a target is occluded for a period of time prior to movement onset however (i.e., memory-guided reaching), the response can no longer be specified in an egocentric visual frame (c.f. Flanders et al., 1992); instead, target location is thought to be encoded via visual cues surrounding the target that are independent of the performer (i.e., an allocentric frame of reference) (Hu & Goodale, 2000). It is therefore not surprising that pointing to a previously visible target presented within a neutral visual background suffers significant degradation in endpoint accuracy. After all, the neutral background does not provide the requisite visual cues to support the scene-based integration of target location. Hence, an important question in the visuomotor control literature pertains to the degree to which contextual features surrounding a target might facilitate memory-guided action.

It is, of course, clear from the visual illusions literature that visual context surrounding a target can impact memory-guided action. Indeed, a number of studies have shown that interposing a period of delay between the disappearance of a target within an illusory background (e.g., size-contrast or induced displacement illusions) and the cueing of a response elicits a robust bias in pointing direction (Bridgeman, Gemmer, Forsman, & Huemer, 2000; Bridgeman, Peery, & Anand, 1997; de Grave, Brenner, & Smeets, 2004; Gentilucci, Chieffi, Deprati, Saetti, & Toni, 1996; Heath et al., 2004; Heath & Rival, 2004; Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000). Visually guided actions however, have been found to elicit greater visuomotor resistance to cognitive illusions relative to memory-guided ones (Aglioti,

De Souza, & Goodale, 1995; Danckert, Sharif, Haffenden, & Goodale, 2002; Haffenden & Goodale, 2002; Westwood et al., 2000, 2001). These findings underscore the notion that visually and memory-guided actions differ with respect to their frames of reference and specification of object metrics. Visually guided actions are thought to be resistant to visual illusion because they are subserved by dedicated visuomotor networks in the dorsal visual pathway that specify absolute (i.e., Euclidean) object metrics with respect to the observer (see Milner & Goodale, 1995 for a review). In other words, the online visuomotor system is thought to use an egocentric frame of reference that computes veridical position of the effector and target without the integration of contextual cues from the entire visual scene. Because the location of the performer and target can change unexpectedly, egocentric coordinates are thought to be available to the motor system only on a moment-to-moment basis (Westwood & Goodale, 2003). Thus, it has been argued that perceptual mechanisms residing in the ventral visual pathway assemble and maintain a relative (i.e., non-Euclidean) and scene-based (i.e., allocentric) representation of the visual world to control memory-guided action. Indeed, the scene-based nature of information supporting memory-guided actions is thought to render such movements susceptible to visual illusions.

As mentioned above, visually guided actions generally demonstrate greater visuomotor resistance to illusory-arrays than memory-guided ones; however, it is important to note that the former are not entirely refractory to illusory arrays. Indeed, a number of studies have shown that pointing/grasping movements under direct visual control can elicit small but reliable illusory-effects (de Grave et al., 2004; Glover & Dixon, 2001; Heath & Rival, 2004; Meeghan et al., 2004; Westwood et al., 2000). These results suggest that although predominately specified via an egocentric visual frame, visually guided reaching control entails a degree of aggregation from allocentric visual cues.

The notion that egocentric and allocentric frames of reference together support the planning and control of visually guided action is consistent with several studies reporting that geometric objects or contextual features – apart from illusory arrays – surrounding a target can facilitate the accuracy of visually guided action. For example, Conti and Beaubaton (1980) and Velay and Beaubaton (1986) reported that participants were more accurate when they pointed to a visible target embedded within a grid-like pattern (i.e., a contextual environment) than when the visible target was presented in a neutral visual environment. More recently, Coello and Greally (1997) have shown that a visible target placed in a wide and structured visual field allowed for highly accurate feedback-based amendments to the reaching trajectory particularly when continuous visual input from the moving limb is available during the response. Importantly, these studies demonstrate that contextual information surrounding a target (i.e., allocentric cues) in combination with vision of the moving limb (i.e., egocentric cues) serve to facilitate accuracy.

Of interest in the present investigation is the degree to which visual structure surrounding a target might influence the kinematics of reaching to a remembered target. Indeed, it has been shown that perceived (Carrozzo, Stratta, McIntyre, & Lacquaniti, 2002) or physical structure (Barry, Bloomberg, & Huebner, 1997; Lemay, Bertram, & Stelmach, 2004) surrounding a remembered target location can facilitate the accuracy

of memory-guided action. However, previous studies did not address whether or not a VB might facilitate (or interfere) with the accuracy of memory-guided reaching movements performed across a range of delay intervals. Indeed, research examining the accuracy of memory-guided reaches produced in an otherwise empty or neutral visual background (e.g. Westwood et al., 2001; Westwood, Heath, & Roy, 2003) has demonstrated that endpoint error and response variability accumulates significantly following even the briefest of delays (i.e., 0 ms). Hence, in the present investigation we examined the kinematics and the endpoint accuracy of visually guided, open-loop, and brief (0 ms) and longer (1000 ms) memory-guided reaching conditions to determine if contextual cues surrounding a remembered target might provide a more robust representation of the target's location in peripersonal space. The brief (0 ms) and longer (1000 ms) delay intervals used here were chosen because previous work has shown such delays to be sensitive to a time-linked increase in endpoint error and variability (Elliott, 1988; Heath & Westwood, 2003; Heath et al., 2004; Westwood et al., 2000, 2001, 2003). Additionally, we sought to determine whether contextual cues surrounding a visible or remembered target might influence putative online interactions between egocentric and allocentric visual frames, thus leading to reaching movements that are controlled more online than reaches performed without a VB. Importantly, in all experimental conditions participant's vision of the movement effector was available to provide a reference point for egocentric comparisons.

In terms of potential research outcomes, if visual structure surrounding a target facilitates the scene-based integration of target information then reaching to a remembered target following a delay should result in a less dramatic accumulation in endpoint error relative to a situation in which contextual features are unavailable. Moreover, vision of a VB should provide the motor system with additional allocentric information about target location, thus in addition to reducing movement error, the VB should provide additional allocentric cues that facilitate the online control of reaching movements.

2. Methods

2.1. Participants

Fourteen volunteers (19–25 years of age) from the Indiana University community volunteered to participate in this study. Participants had normal or corrected-to-normal vision and were right-handed by self-report. Informed consent was obtained in accordance with the Office of Human Research, Indiana University.

2.2. Apparatus

Participants sat at a table (table-top 65 cm above the ground) and completed goal-directed reaching movements with a 10 cm illuminated stylus. Reaching movements were executed from a common start position (i.e., a 1 cm diameter microswitch placed 5 cm from the edge of the table) to midline targets (red LEDs) located 32

(near), 34 (middle), and 36 (far) distal from the start position. In addition, green LEDs (i.e., visual background: VB) were positioned in a 10 cm by 10 cm square around the target LEDs (see Fig. 1). The presentation of target and VB was controlled via an interval-timing device.

2.3. Procedure

Participants were instructed to complete discrete reaching movements “as quickly and accurately as possible” to the illuminated red target in response to an auditory

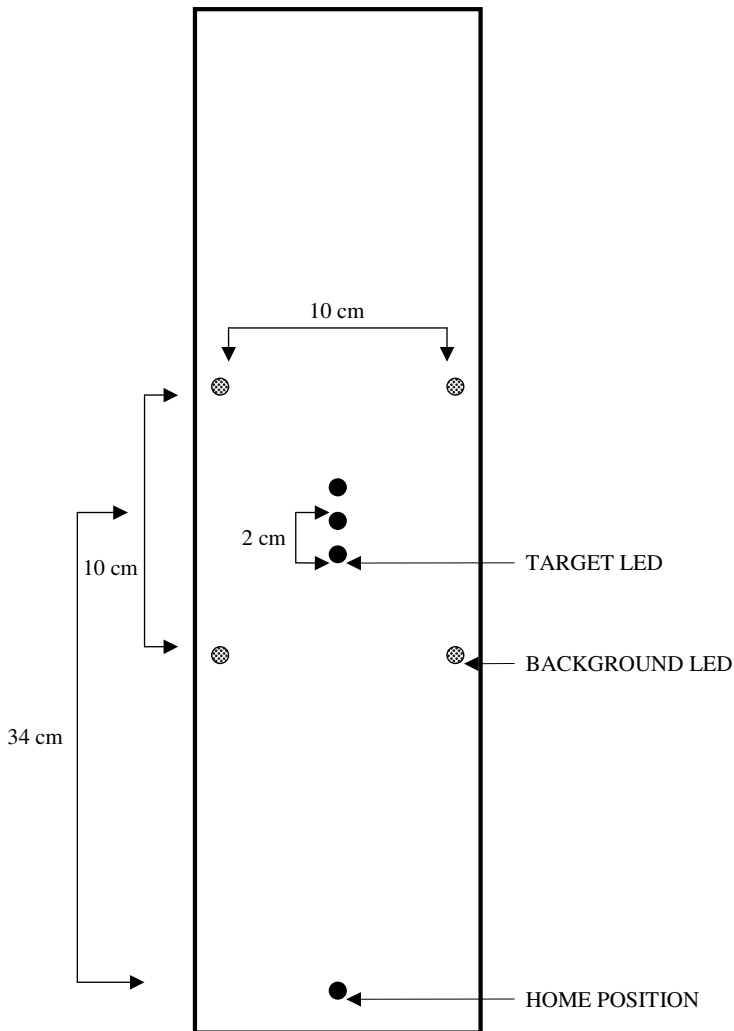


Fig. 1. Diagram of the experimental apparatus.

cue. The experimental session involved two background conditions and four visual conditions (see below). In one background condition, the target LED was presented within an illuminated square (i.e., the VB condition). In the second background condition, the target object, but not the illuminated square was presented (i.e. neutral visual background: NVB). Participants began a trial with their pointing stylus depressing the home position. After the home position was depressed the target LED was illuminated for a 2s preview phase. In addition, the illuminated square was provided at preview and remained illuminated until the end of a VB trial. During NVB trials only the target was presented during preview.

Four visual conditions were factorially arranged within the two background conditions. In the visually guided (VG) condition, following the 2s preview phase, an auditory tone signalled participants to begin their reaching movement and the target LED remained illuminated for the duration of the response. Hence, participants were able to view the position of their moving limb (i.e., the illuminated stylus) relative to the illuminated target and the illuminated VB if available. In the open-loop (OL) condition, immediately following the preview phase, the auditory tone signalled participants to begin their movement, and the target LED was extinguished once the participant had released pressure from the home position microswitch. In this condition, vision of the limb and target was available at movement planning; however, only the limb (and the illuminated square during VB trials) was visible during the response. In the 0ms (D0) and 1000ms (D1000) delay conditions, the target LED was extinguished following the preview phase and the auditory initiation tone was provided coincident with target offset (i.e., the D0 trials) or following 1000ms of delay (i.e., the D1000 trials), thus, vision of the target (but not limb) was extinguished prior to and during the response. Once again, for VB but not NVB trials, vision of the illuminated square was available throughout the reaching response. Knowledge of results was not explicitly provided to participants; however, participants were able to evaluate their terminal accuracy in VG trials.

Background (2) and visual conditions (4) were organized into eight randomly ordered trial blocks, with target distance presented an equal number of times in a pseudo-random fashion. In total participants completed 240 trials.

2.4. Data collection and reduction

A single infra-red emitting diode (IRED) was affixed to the end of the pointing stylus. The position of the IRED was sampled at 200 Hz for 2s following the auditory initiation tone using an OPTOTRAK 3020 system (NDI, Waterloo, ON, Canada). Offline raw displacement data were filtered with a second order dual-pass Butterworth filter using a low-pass cut-off frequency of 10 Hz. Instantaneous velocities were determined by differentiating displacement using a two-point central finite difference algorithm. Subsequently, acceleration data were obtained by differentiating velocity data. Movement onset was identified as the first frame of 10 consecutive frames (50ms) in which movement velocity exceeded 50 mm/s. Movement offset was identified as the first frame of 10 consecutive frames (50ms) in which movement velocity was less than 50 mm/s.

Dependent variables included: reaction time (RT: time between the auditory initiation cue and movement onset), movement time (MT: time between movement onset and offset), peak velocity (PV: maximum resultant velocity between movement onset and offset), constant error (CE) in the primary (antero-posterior: *Y*-axis) and secondary (medial-lateral: *X*-axis) movement directions and their associated variable error (VE) values (i.e., within-participants standard deviations). Note that a positive CE in the primary movement direction indicated an overshooting error, whereas a negative CE in this movement direction represented an undershooting error. A positive CE in the secondary movement direction indicated greater rightward bias, whereas a negative CE in this movement direction represented greater leftward bias. To examine the temporal symmetry of the velocity profiles, and to investigate the possible use of online control late in the movement (e.g., Khan, Elliott, Coull, Chua, & Lyons, 2002) we computed proportional time after PV (PTAPV: proportion of MT occurring after PV), and proportional time after peak deceleration (PTAPD: proportion of MT occurring after maximum resultant deceleration).

Last, a regression analysis was used to determine the proportion of variability (R^2) in endpoint position that was explained by the spatial position of the limb at PD (e.g., Binsted & Heath, 2004; Elliott et al., 1999; Heath et al., 2004). It has been previously shown that if participants are engaged in online, feedback-based control, then the position of the limb at this point in the reaching trajectory need not be strongly predictive of the ultimate movement endpoint as errors of distance and direction (e.g., undershooting/overshooting or leftward/rightward bias) are detected and corrected online. If, however, participants planned their reaching movement primarily in advance of movement onset, then the spatial position of the limb at PD should be significantly related to the ultimate movement endpoint (e.g., errors in the initial movement are not corrected and thus gradually build throughout the response). By comparing the R^2 values for VB and NVB reaches at PD, we sought to determine whether the presence of the VB facilitated the online control of the reaching trajectory.

3. Results

All omnibus tests were interpreted using an α level of 0.05. Significant effects/interactions requiring post-hoc examination were subjected to simple effects analyses and a Bonferroni correction for multiple comparisons ($\alpha < 0.05$). Only significant effects are reported here.

3.1. Performance measures

RT, MT, CE, and VE data were subjected to 2 (background condition: VB, NVB) by 4 (visual condition: VG, OL, D0, D1000) by 3 (target distance: near, middle, far) fully repeated-measures ANOVAs.

Examination of RT yielded effects for visual condition, $F(3, 39) = 5.25$, $p < 0.01$, and target distance, $F(2, 26) = 8.33$, $p < 0.01$. OL trials (242 ms) and D1000 trials

(253 ms) had longer RTs than D0 trials (221 ms); VG trials (238 ms) did not differ from the other visual conditions. The effect for target distance indicated that RTs for the near target (242 ms) were longer than middle (237 ms) and far targets (236 ms), which did not differ.

The MT analysis revealed main effects for background, $F(1, 13) = 8.01, p < 0.02$, visual condition, $F(3, 39) = 7.37, p < 0.001$, and target distance, $F(2, 26) = 25.91, p < 0.001$. The effect of background indicated that VB trials (462 ± 18 ms) had longer MTs than NVB trials (444 ± 16 ms). The effect for visual condition revealed that VG (475 ± 16 ms) and D1000 (463 ± 18 ms) trials elicited longer MTs than OL

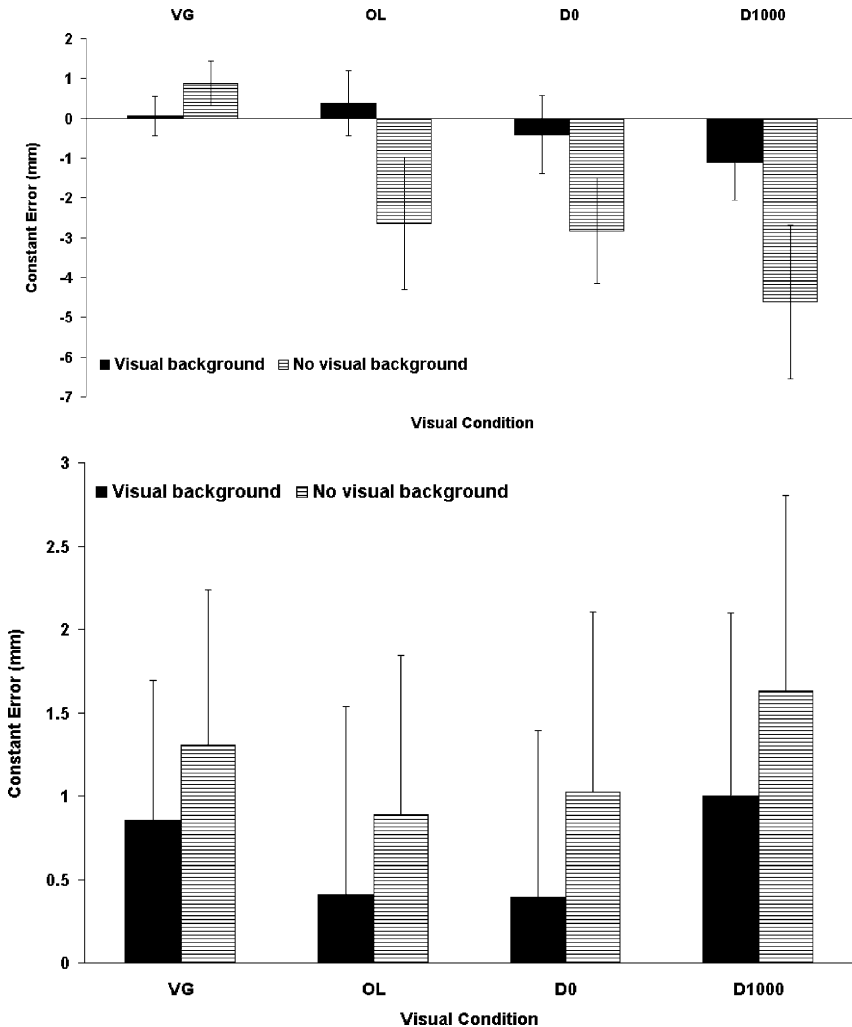


Fig. 2. Constant error (mm) in the primary (top panel) and secondary (bottom panel) movement directions as a function of background and visual condition. Error bars represent the standard error of the mean.

(437 ± 17 ms) or D0 (439 ± 19 ms) trials (which did not differ). The effect for target distance revealed the expected linear increase in MT as a function of movement amplitude (significant linear effect: $F(1, 13) = 8.01$, $p < 0.02$) (e.g., Westwood et al., 2003).

The analysis of CE in the primary movement direction revealed main effects for background, $F(1, 13) = 5.07$, $p < 0.05$, visual condition, $F(3, 39) = 4.29$, $p < 0.02$, and target distance $F(2, 26) = 4.09$, $p < 0.03$. The effect for background indicated that VB trials (-0.3 ± 0.6 mm) were more accurate than NVB trials (-2.3 ± 1.12 mm). The effect for visual condition indicated that VG trials were more accurate than D0 and D1000 trials ($p < 0.05$); OL through D1000 trials did not differ from one

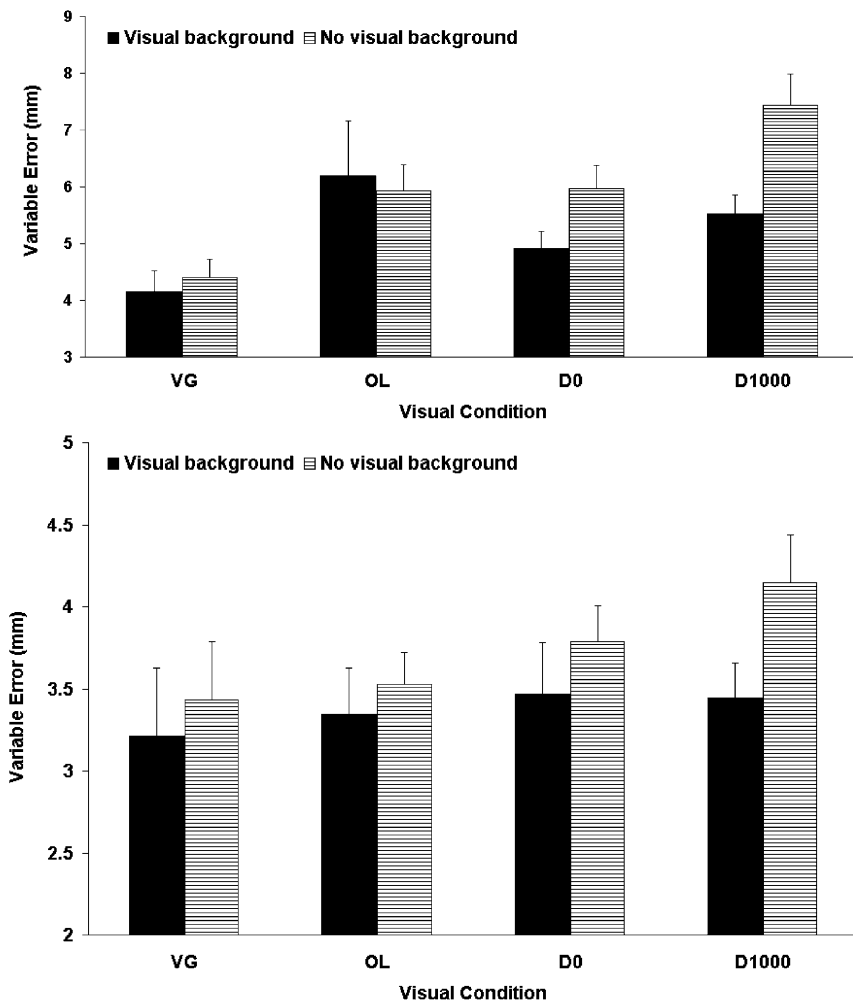


Fig. 3. Variable error (mm) in the primary (top panel) and secondary (bottom panel) movement directions as a function of background and visual condition. Error bars represent the standard error of the mean.

another ($p > 0.05$). The effect for target indicated that reaches to the near target were more accurate than reaches to the middle or far target (significant second-order polynomial, $F(1, 13) = 9.91$, $p < 0.01$).

The results for CE in the secondary movement direction elicited main effects for background condition, $F(1, 13) = 6.05$, $p < 0.03$, and target distance, $F(2, 26) = 28.70$, $p < 0.001$. NVB trials (1.21 ± 0.9 mm) exhibited greater rightward bias than VB trials (0.66 ± 0.9 mm) and the effect for target distance indicated that directional error increased with target eccentricity (significant linear effect: $F(1, 13) = 40.63$, $p < 0.001$) (Fig. 2).

The analysis of VE in the primary movement direction revealed a main effect for visual condition, $F(3, 39) = 7.37$, $p < 0.001$: VG (4.29 ± 0.26 mm) trials were less variable than OL (6.02 ± 0.53 mm) or D0 (5.43 ± 0.30 mm) trials, which in turn were less variable than D1000 trials (6.81 ± 0.32 mm). The examination of VE in the secondary movement direction yielded an effect for background condition, $F(1, 13) = 6.61$, $p < 0.03$: VB trials (3.3 ± 0.25 mm) were less variable than NVB trials (3.8 ± 0.20 mm) (Fig. 3).

3.2. Kinematic measures

We analyzed PV, PD, PTAPV, and PTAPD using 2 (background condition: VB, NVB) by 4 (visual condition: VG, OL, D0, D1000) by 3 (target distance near, middle, far) full-repeated measures ANOVA.

Analysis of PV revealed main effects for visual condition, $F(3, 39) = 3.19$, $p < 0.04$, and target distance, $F(2, 26) = 269.93$, $p < 0.001$. PVs for OL trials (1546 ± 61 mm/s) were greater than D1000 trials (1463 ± 73 mm/s): VG (1515 ± 61 mm/s) and D0 (1517 ± 66 mm/s) trials did not differ from the former conditions. The effect for target distance indicated PV increased in relation to increasing target distance (significant linear effect: $F(1, 13) = 332.72$, $p < 0.001$). Examination of PD indicated a main effect for target distance, $F(2, 26) = 6.54$, $p < 0.01$. Specifically, PD increased as a function of increasing target amplitude (significant linear effect: $F(1, 13) = 7.45$, $p < 0.02$).

The analysis of PTAPV yielded a main effect for visual condition, $F(3, 39) = 4.45$, $p < 0.01$, indicating that VG trials (0.63 ± 0.01) spent proportionately more time after PV than OL (0.61 ± 0.1), D0 (0.61 ± 0.1), or D1000 (0.60 ± 0.01) trials (which did not differ from one another). The analysis of PTAPD revealed an effect for background condition, $F(1, 13) = 5.61$, $p < 0.04$, visual condition, $F(3, 39) = 9.92$, $p < 0.001$ and target distance, $F(2, 26) = 3.47$, $p < 0.05$. The effect for background demonstrated that VB trials (0.36 ± 0.02) spent a greater proportion of the reaching trajectory post peak deceleration than NVB trials (0.34 ± 0.02). The results for visual condition mirrored the findings for PTAPV (see above). PTAPD was found to increase with greater target amplitude (significant linear effect, $F(1, 13) = 10.20$, $p < 0.01$).

3.3. Proportion of endpoint variance explained at PD

These analyses examined the proportion of variance (R^2) in movement endpoints explained by the position of the limb at PD. Accordingly, R^2 values (primary and

secondary movement directions) were subjected to 2 (background condition: VB, NVB) by 4 (visual condition: VG, OL, D0, D1000) by 3 (target distance: near, middle, far) fully repeated-measures ANOVA. The results in the primary movement direction yielded no significant effects or interactions. In the secondary movement direction, a main effect for background condition was produced, $F(1, 13) = 10.88$, $p < 0.01$. Specifically, R^2 values for VB reaches (0.41) were less than NVB reaches (0.47).

4. Discussion

4.1. *The impact of visual condition*

The results for CE in the primary movement direction indicated that VG trials were more accurate than D0 or D1000 trials: no differences in CE were found between OL, D0, and D1000 trials. Examination of VE in the primary movement direction indicated VG reaches were less variable than OL and D0 reaches, in turn OL and D0 reaches were less variable than D1000 reaches. In the secondary movement direction however, CE and VE were not influenced by the different visual conditions. The fact that VG and OL trials elicited comparable endpoint accuracy is consistent with a limited number of studies (Carlton, 1981; Elliott, 1988; Heath & Westwood, 2003). It is, however, important to note that OL trials produced greater endpoint variability than VG trials, suggesting reaches performed without continuous visual contact from the target were not as metrical as their visually guided counterparts. One reason for the difference between VG and OL trials might relate to the fact that during VG trials (but not OL trials) visual feedback from a completed trial was available to participants to improve offline planning of a subsequent response (Khan et al., 2002; Khan, Lawrence, Franks, & Buckholz, 2004). In addition, the more metrical response of VG trials underscores the importance of continuous visual feedback from the reaching environment to implement highly accurate online error detection and correction mechanisms (Chua & Elliott, 1993; see Elliott et al., 2001 for review).

Comparison between OL and memory-guided conditions did not produce reliable differences in endpoint accuracy or variability. At the outset, this result counters previous findings (e.g., Elliott, 1988; Elliott, Carson, Goodman, & Chua, 1991) and some of our own recent work reporting that movement error accumulates over increasing memory delays due to a time-linked decay of target information (Heath et al., 2004; Westwood et al., 2001, 2003). Importantly, however, past research probing the consequence of increased memory delays on reaching performance employed occlusion techniques wherein vision of target and hand were withdrawn concurrently (i.e., via turning off the room lights or visual occlusion goggles) (see Elliott, 1988; Elliott et al., 1991; Heath et al., 2004; Westwood et al., 2001; Westwood et al., 2003). Such manipulations are problematic because they cannot disentangle the putative contributions of visual limb and visual target delays. Certainly, however, this represents an important issue in the memory-guided reaching literature in light of Prablanc and colleagues (e.g., Prablanc, Echallier, Jeannerod, & Komilis, 1979)

seminal observations that seeing one's limb prior to a response results in reaches that are more accurate and less variable than when vision of the limb is withdrawn prior to the response.

In the present investigation, the effect of increasing delays of limb information was removed from the effect of increasing delays of target information by always providing participants with veridical limb information. As outlined above, this manipulation resulted in comparable accuracy and variability across OL, D0 and D1000 conditions. Moreover, the moderate R^2 values associated with OL through D1000 trials suggests that such actions engaged in a mode of online control on par to that of VG trials (cf. Heath, submitted for publication; Heath & Westwood, 2003). On the basis of this and other research, we propose that a stored target representation provided the motor system a reasonably accurate and temporally durable (i.e., up to 1000 ms of delay) referent for online control. Moreover, the present findings argue that the time-sensitive decay in reaching accuracy reported in earlier studies is not related to a slow decay of stored target information. Instead, it is proposed that decreased initial limb coordinate estimation contributed to the time-sensitive increase in reaching error reported in earlier work.

4.2. *The Influence of a visual background*

Recall that a limited number of studies have reported that contextual cues surrounding a visible or remembered target enhanced the accuracy of reaching movements (Barry et al., 1997; Carrozzo et al., 2002; Coello & Greally, 1997; Conti & Beaubaton, 1980; Lemay et al., 2004; Velay & Beaubaton, 1986). For instance, Conti and Beaubaton showed that the presence of a VB decreased the radial error associated with VG reaching movements, a finding Velay and Beaubaton later attributed to the fact that background cues improve online, feedback-based reaching control. In a similar vein, Lemay et al. reported that reaches to a remembered target (i.e., 12 s of visual delay) embedded within a VB were more accurate and less variable than memory-guided reaches performed in the absence of a VB. Furthermore, Lemay et al.'s findings indicated that trials performed with a VB exhibited longer deceleration times than their non-VB counterparts (cf. Carrozzo et al., 2002). More evidence for the positive impact of a VB on movement accuracy is found in the work of Coello and Greally (1997) who demonstrated that decreasing the size of the visual field and removing VB information decreased movement accuracy. Hence, there is sufficient evidence from the research to suggest that a VB facilitates the accuracy of VG and memory-guided actions via the evocation of effective, visually based amendments to the reaching trajectory.

Recall that the present investigation sought to examine the impact of a VB over a range of visually guided, open-loop, and delay intervals. To our knowledge, this represents the first systematic investigation to examine whether a VB improves the stability of memory-guided reaches over increasing memory delays. Toward this end, we found that VB trials were more accurate and less variable than their NVB counterparts regardless of whether the target was visible during the reaching movement (i.e., VG trials), occluded at movement onset (i.e., OL trials), or occluded for 0 or

1000ms prior to response cueing (i.e., D0 and D1000 trials). Moreover, an explicit goal of this investigation was to test the assumption that VB reaches were controlled online to a greater extent than NVB reaches. In pursuit of this goal, we found that VB trials were associated with longer MTs and spent a greater proportion of total reaching time post peak deceleration: a finding that has been interpreted as evidence for online corrections late in the reaching trajectory (e.g., Khan et al., 2002). Additionally, we examined the spatial correlation (R^2 values) between the position of the limb at peak deceleration and the ultimate movement endpoint in the primary and secondary movement directions. Recall that the underlying logic of this technique is that movements executed with minimal feedback-based control should unfold according to the spatiotemporal characteristics specified in advance of the movement, thereby yielding moderate to robust R^2 values. In contrast, reaches controlled primarily via feedback-based processes should yield weak R^2 values as errors in amplitude and/or direction are detected and corrected online (see Binsted & Heath, 2004; Heath et al., 2004 for complete details). The results of these analyses indicated that VB reaches in the secondary movement direction exhibited weaker R^2 values relative to their non-VB counterparts, thus suggesting that VB reaches used online control mechanisms to a greater extent than NVB reaches in regulating the directional accuracy of the reaching movement. Interestingly, however, R^2 values in the primary movement direction did not differ between VB and NVB trials.

The fact that R^2 values differentiated between background conditions in the secondary but not primary movement direction suggests that the VB had a primary influence on improving the online directional control of reaching movements. Such a finding is congruent with Georgopolous' (1991) proposal that movement amplitude and direction are subserved by functionally distinct visuomotor channels. Supporting Georgopolous' hypothesis, research by Barry et al. (1997) examining memory-guided reaches (i.e., 2–4s of visual delay) to a remembered target embedded in a VB demonstrated that directional accuracy was impacted by VB availability to a greater extent than amplitude accuracy. In the present experiment, our results for CE and VE demonstrated an equal effect for the VB in both movement directions, in spite of this, our R^2 analyses suggest that online control mechanisms may be differentially impacted by VB availability, at least in terms of within-movement modifications.

A major theoretical issue remains to be resolved: how does a visual background facilitate the accuracy and online control of VG, OL and memory-guided reaches? Previous research has demonstrated that effector/target comparisons assist in optimizing reaching accuracy (Beggs & Howarth, 1972; Carlton, 1979; Crossman & Goodeve, 1983; Keele, 1981). With regard to memory-guided reaches, egocentric comparisons between the movement effector and remembered target location have been hypothesized to allow reasonably accurate reaching movements to occur when a target is occluded (Carlton, 1981; McIntyre, Stratta, & Lacquaniti, 1997, 1998). Certainly, this idea is consistent with Heath and Westwood (2003) who demonstrated that participants are able to make accurate comparisons between a limb and a stored sensory target representation to affect reasonable accurate feedback-based corrections.

We propose that vision of a VB facilitates movement accuracy by providing allocentric information about target location in addition to providing an enhanced reference for egocentric judgements between the movement effector and the visible or the remembered target location. Although egocentric effector/target comparisons were not always available in the present investigation (i.e., OL, D0, D1000 trials), egocentric effector/VB comparisons and allocentric target (visible or remembered)/VB comparisons were possible across all VB trials (i.e., VG, OL, D0, D1000), thereby providing a basis for improving overall reaching accuracy. Indeed, our results compliment Carrozzo et al. (2002) who found that when participants were made aware of an allocentric relationship between target locations they were more accurate than a condition wherein these comparisons were not available. From their results, Carrozzo and colleagues concluded that participants used allocentric judgements about target location to facilitate the accuracy of their reaching movements. Based on the present results, we propose that allocentric comparisons between target (visible or remembered) and VB allowed for enhanced target localization in peripersonal space. Participants could then use this enhanced target representation to implement enhanced egocentric comparisons between the limb and target (visible or remembered) to facilitate online control and endpoint accuracy. Importantly, our results show that these egocentric and allocentric comparisons are possible for both visually guided and memory-guided reaching conditions.

The notion that allocentric and egocentric visual frames interact to influence the trajectory of reaching movements is counter to a strict interpretation of the perception/action model (PAM: Milner & Goodale, 1993). Indeed, an early variant of the PAM asserts that visually guided reaches are mediated by dedicated visuomotor mechanisms residing in the posterior parietal cortex (PPC) of the dorsal visual pathway that compute the real time location of a target in egocentric visual frames of reference. When vision of the aiming environment is withdrawn however, the normally online operation of the visuomotor system is disrupted and an allocentric target representation is thought to be formulated by perception-based mechanisms residing in the inferotemporal lobe of the ventral visual pathway. Importantly, the functional and anatomical dissociation between dorsal and ventral visual processing is thought to preclude aggregation of egocentric and allocentric visual frames for movement planning and control. More recent formulations of the PAM however, favour the interaction between dorsal and ventral visual processing mechanisms (Goodale & Westwood, 2004). Indeed, Whitney, Westwood, and Goodale (2003) recently demonstrated that a vertically drifting background (i.e., a distant motion signal) produced continuous updating of reaching movements to a stationary target. This finding strongly suggests that multiple frames of reference can be incorporated by online control mechanisms within the PPC (Desmurget et al., 1999; Pisella et al., 2000), to influence the online, feedback-based control of reaching movements.

4.3. Conclusions

In sum, we have demonstrated that vision of a VB can facilitate reaching accuracy and reduce movement variability for VG, OL, and reaches made after brief visual

delays. Our results also indicate that VB availability enhances directional online control to a greater extent than amplitude online control during the later stage of a reaching movement. Furthermore, our results indicate that vision of a VB provides allocentric information about the target location that can be used in conjunction with egocentric limb, VB, and visible or stored target information to facilitate online control processes.

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